Globicephaline whales from the Mio-Pliocene Purisima Formation of central California, USA

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Oceanic dolphins (Odontoceti: Delphinidae) constitute the most speciose family of extant cetaceans, yet their fossil record is limited. Although several extinct species are known from Mediterranean and North Atlantic localities, there are few examples from deposits along the Pacific Rim. Despite the rich record of successive marine mammal fossil assemblages in the extensively sampled eastern North Pacific, only one fossil delphinid, *Protoglobicephala* (Pliocene, Baja California), has been described. We report globicephaline remains from the Mio-Pliocene Purisima Formation of Northern California, including a partial cranium and two isolated petrosals. The skull exhibits large ridges on the premaxillae, and cannot be referred to any extant globicephaline genus. Similarly, the petrosals cannot be referred to any described delphinid genus, although they are most similar to those of *Globicephala*. Linear regression analyses demonstrate that promontorium length and bony nares width scale significantly within delphinidans, and provide a new method for testing referrals of isolated fossil odontocete petrosals to taxa known only by crania. Applying this method to the new globicephalines from the Purisima Formation, we find the petrosals to be too small to represent the same taxon as the skull, thus indicating the presence of two separate species. Our results demonstrate that globicephalines had achieved a worldwide distribution by the early Pliocene, suggesting diversification of the subfamily by 5 Ma.

Key words: Mammalia, Cetacea, Odontoceti, Delphinidae, Globicephalinae, Pliocene, Purisima Formation, California.

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Introduction

Although large-bodied, cosmopolitan, and conspicuously present in modern oceans and marine parks, dolphins of the delphinid subfamily Globicephalinae have a meager fossil record. Globicephalines, also known as “blackfish”, include several modern species typically characterized by dark or black external pigmentation, large body size, a blunt rostrum, a large melon, and a low tooth count (Le Duc 2009). Recent phylogenetic hypotheses based on molecules have consistently found globicephalines to be monophyletic; however, hypothesized relationships within this clade vary (contrast McGowen 2011 with Cunha et al. 2011 and Vilstrup et al. 2011), and different studies disagree on the inclusion of the killer whale *Orcinus orca* (Le Duc et al. 1999; McGowen 2011; but see Vilstrup et al. 2011 and Cunha et al. 2011). Morphology-based cladistic analyses typically also recover a monophyletic Globicephalinae (but see Murakami et al. 2012a, b) and include *Orcinus* as a member (Bianucci 2005; Aguirre Fernandez et al. 2009; Geisler et al. 2011: fig. S1).

Although delphinids as a whole are geographically widespread and represent the most diverse family of extant cetaceans, their fossil record is limited and challenging to interpret. Few detailed studies on the skeletal morphology of extant delphinids (e.g., Perrin 1975) exist, and the paucity of recognized osteological characters to differentiate the many extant, small-bodied delphinids has hampered interpretation of their fossil relatives (Whitmore 1994; Pichler et al. 2001). Fossil globicephalines, although rare, may be easier to assess, because they are characterized by more obvious morphological differences than exist between the extant taxa (Bianucci 2005; Aguirre Fernandez et al. 2009).

Recent molecular hypotheses of delphinid phylogeny have yielded varying tree topologies with short internal branch lengths, usually interpreted as the result of a late Neogene explosive radiation (McGowen et al. 2009; McGowen

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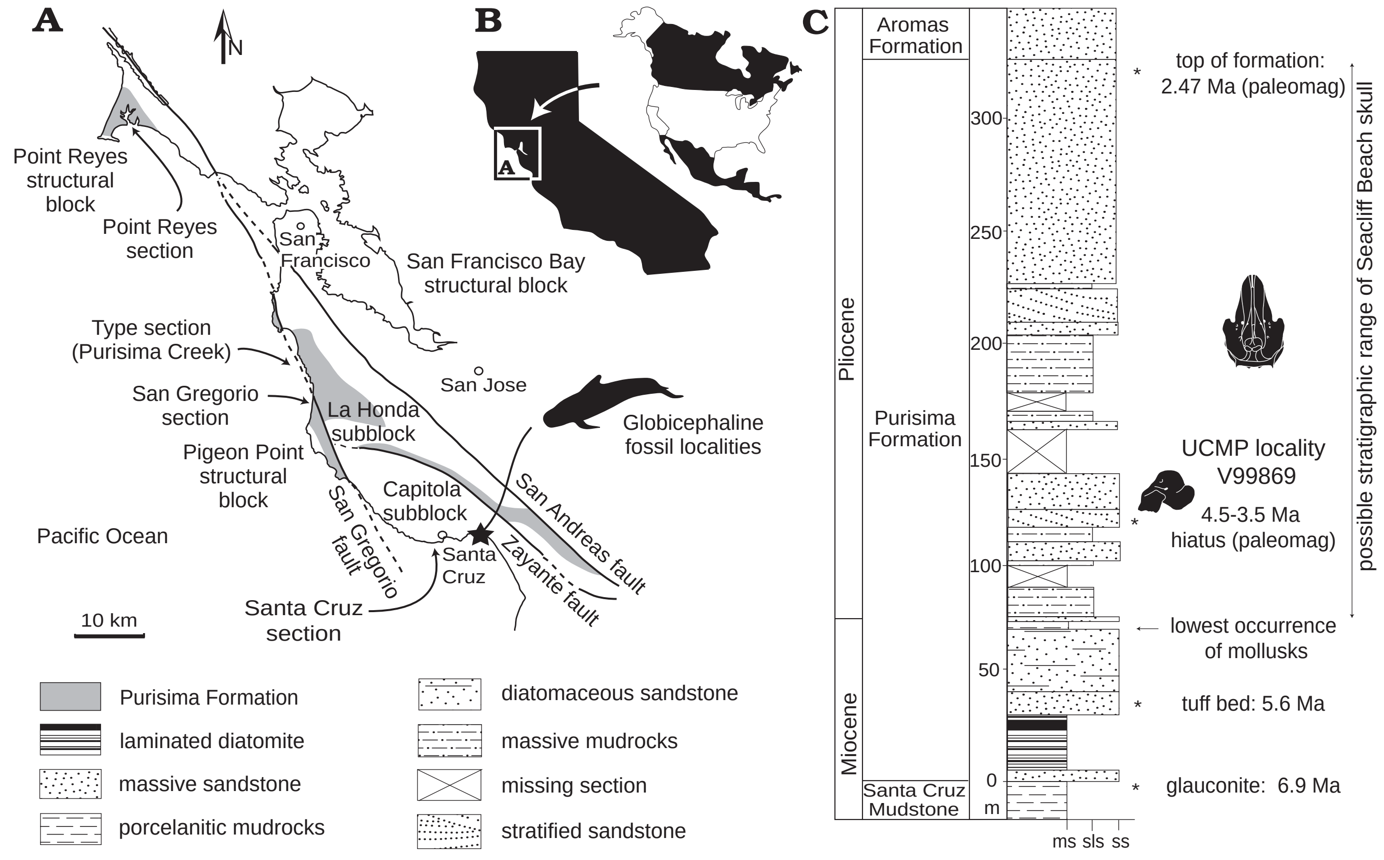

Fig. 1. Geographic and stratigraphic context of Purisima Formation fossil globicephalines. **A**. Geologic map of Purisima Formation exposures in Northern California (modified from Boessenecker 2011). **B**. Location of inset map in California and North America. **C**. Stratigraphic column of the Santa Cruz section of the Purisima Formation, showing stratigraphic control of globicephaline fossils (modified from Powell et al. 2007 and Boessenecker and Perry 2011). Skull and petrosal symbols indicate stratigraphic position of fossils reported herein. Abbreviations: ms, mudstone; sls, siltstone; ss, sandstone. Asterisks denote age determinations.

2011; Vilstrup et al. 2011). The ability of various delphinids to produce fertile interspecific hybrids and the morphological similarity of many delphinids are also reflective of a rapid and relatively recent diversification (Aguirre Fernandez et al. 2009), the timing of which has been a matter of debate (McGowen et al. 2009; Vilstrup et al. 2011). The study of fossil delphinids allows hypotheses regarding the timing of delphinid cladogenesis to be tested, in addition to documenting the extinct morphological diversity of this group (e.g., Fordyce et al. 2002; Bianucci 1996, 2005; Aguirre Fernandez et al. 2009; Post and Kompanje 2010). The purpose of this study is to describe a globicephaline cranium and isolated petrosals from the Mio-Pliocene Purisima Formation of northern California (Fig. 1), and to discuss the bearing of the globicephaline fossil record on the origin of the clade.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; CAS, California Academy of Sciences, San Francisco, USA; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, USA; UCMP, University of California Museum of Paleontology, University of California, Berkeley, USA; USNM, United States National Museum of Natural History, Washington D.C., USA.

Material and methods

To ascertain whether the isolated petrosals are referable to the taxon represented by the skull, we examined the relationship between petrosal size and skull size by means of a reduced major axis regression analysis performed in PAST (Hammer 2001). Our dataset consisted of measurements from 62 individual delphinidans (20 extant, 14 extinct species; see SOM, Supplementary Online Material available at http://app.pan.pl/SOM/app60-Boessenecker_etal_SOM.pdf). Two measurements could be applied to the Purisima Formation globicephalines: (i) length of the promontorium, and (ii) maximum width of the external bony nares. The length of the promontorium was measured as described in Geisler and Sanders (2003: 116), from the anteroventral margin of the fenestra rotunda to the anterior margin of the pars cochlearis.

Geological setting

UCMP 219223, hereafter referred to as the Seacliff Beach skull, was preserved within a small sandstone boulder, discovered by Robin Eisenman (Aptos, California, USA) on a beach along the northern shore of Monterey Bay (UCMP locality V99879; Fig. 1). The dark color and preservation of the bone, the lithology of the associated matrix, and associated invertebrate fossils indicate that the fossil had eroded from outcrops of the nearby Purisima Formation. In the Monterey Bay area, the Purisima Formation consists of a 300 meter thick package of "blue" sandstone, siltstone, and diatomite beds, with glauconitic and phosphatic bone beds that were deposited in offshore, transition zone, shoreface, and foreshore environments, reflecting an overall regression.

The Purisima Formation dates from the latest Miocene and Pliocene, ranging from 6.9 to 2.47 Ma in age (Powell et al. 2007). Glauconite from the basal unconformity has been K/Ar dated to 6.9 ± 0.5 Ma, while an ash bed approximately 25 m above the base of the formation has been chemically correlated with other ash beds in California, and is approximately 5.0 ± 0.3 Ma in age (Powell et al. 2007). In addition, paleomagnetostratigraphy indicates that the "pebble marker bed" of Madrid et al. (1986) (= UCMP locality V99869) marks a ca. 1 Ma hiatus in deposition from 4.5–3.5 Ma (Madrid et al. 1986). A diverse assemblage of marine fossils has been recovered from the Purisima Formation, including mollusks, echinoderms, crustaceans, fishes, birds, pinnipeds, cetaceans, and a sirenian (Kellogg 1927; Mitchell 1962; Nations 1975; Barnes 1977; Repenning and Tedford 1977; Domning 1978; Barnes 1985; Perry 1988; Powell 1998; Stewart and Perry 2002; Boessenecker 2006, 2011; Whitmore and Barnes 2008; Boessenecker and Perry 2011; Boessenecker and Smith 2011).

The Seacliff Beach skull could have eroded either from submerged offshore outcrops of the Purisima Formation, or from nearby coastal cliffs. Although the exact source outcrop cannot be ascertained, fossil invertebrates and the lithology of the associated matrix constrain its stratigraphic position. Mollusks are rare in the basal 60 meters of the Purisima Formation, an interval corresponding to the latest Miocene (Powell et al. 2007), but abundant from above this horizon to the top of the formation. Mollusks preserved within the concretion of the Seacliff Beach skull include small indeterminate bivalves, partial shells of *Crepidula* sp., and large specimens of *Anadara trilineata*. Strata including numerous specimens of both *Anadara trilineata* and *Crepidula* occur at the Crab Marker Horizon (sensu Madrid et al. 1986; ~75 meters above the base of the Purisima Formation; Powell et al. 2007: fig. 2), the "Upper Shell Bed Facies" of Perry (1988; ~115–125 meters above the base of the Purisima Formation) and the "*Crepidula* Facies" of Perry (1988; ~125–145 meters above the base of the Purisima Formation). Available evidence indicates the Seacliff Beach skull originated from at least 60 meters above the base of the Purisima Formation but below its upper contact (~300 meters) with the Aromas Formation (Fig. 1A), approximately constraining an age of 5.0–2.47 Ma, or earliest Pliocene to late Pliocene (Zanclean–earliest Gelasian).

Additionally, two globicephaline petrosals from the Purisima Formation (described and tentatively referred herein to a second globicephaline taxon) were collected in situ from the pebble marker bed (UCMP locality V99869), which is 4.5–3.5 Ma (early Pliocene, Zanclean) in age based on paleomagnetism (Madrid et al. 1986; Powell et al. 2007). Detailed locality data are available from UCMP upon request.

Systematic palaeontology

Mammalia Linneaus, 1758
Cetacea Brisson, 1762
Odontoceti Flower, 1867
Delphinidae Gray, 1821
Globicephalinae Gray, 1850
Gen. et sp. indet. 1

Figs. 2–4.

Material.—UCMP 219223 (the Seacliff Beach skull), a fragmentary skull collected from UCMP locality V99879, northern shore of Monterey Bay, USA, by Robin Eisenman. Mio-Pliocene Purisima Formation, early to middle Pliocene (5–2.47 Ma).

Description

Skull.—Although the "core" portion of the cranium is intact, most of the rostrum and the vertex is missing, as are most of the braincase elements, squamosals, lateral portions of the facial region, pterygoid hamuli, nasals, jugals, and lacrimals (Figs. 2–4). The remaining portions of the skull are well preserved, and include much of the orbital region, medial facial region, anteroventral portion of the braincase, posterior palate, and the internal choanae. The skull is relatively large, with a slightly concave facial plane; if the vertex were complete, the face would likely have appeared more concave. Damage to the skull has exposed a partial endocranial cast. Skull measurements are presented in Table 1. A tentative reconstruction of the Seacliff Beach skull is given in Fig. 4.

Premaxilla.—The preserved rostral surface of the premaxilla is wide, flat, and smooth anteriorly, while tapering posteriorly to form a strongly convex and posterolaterally directed ridge (Fig. 2A). The lateral part of the premaxilla overlaps and is sutured to the maxilla anteriorly. The mesorostral canal is filled with matrix, and anteriorly measures 35 mm deep and 20 mm wide. The anteromedial sulcus lies just medial to the posterior end of the rostral surface of the premaxilla, delineating the elongate prenarial triangle. A large (15 mm wide) premaxil-

Table 1. Measurements (in cm) of the Seacliff Beach skull, UCMP 219223; (e) denotes estimated measurement of incomplete feature.

Measurement	UCMP 219223
Total length (as preserved)	41.50
Depth of rostrum at base	5.57
Maximum width across premaxillary sac fossae	141 (e)
Maximum width of endocast	14.70
Dorsoventral depth of endocast	14.83
Maximum width of external bony nares	11.05
Maximum width of premaxillae at anterior end of rostrum	10.15

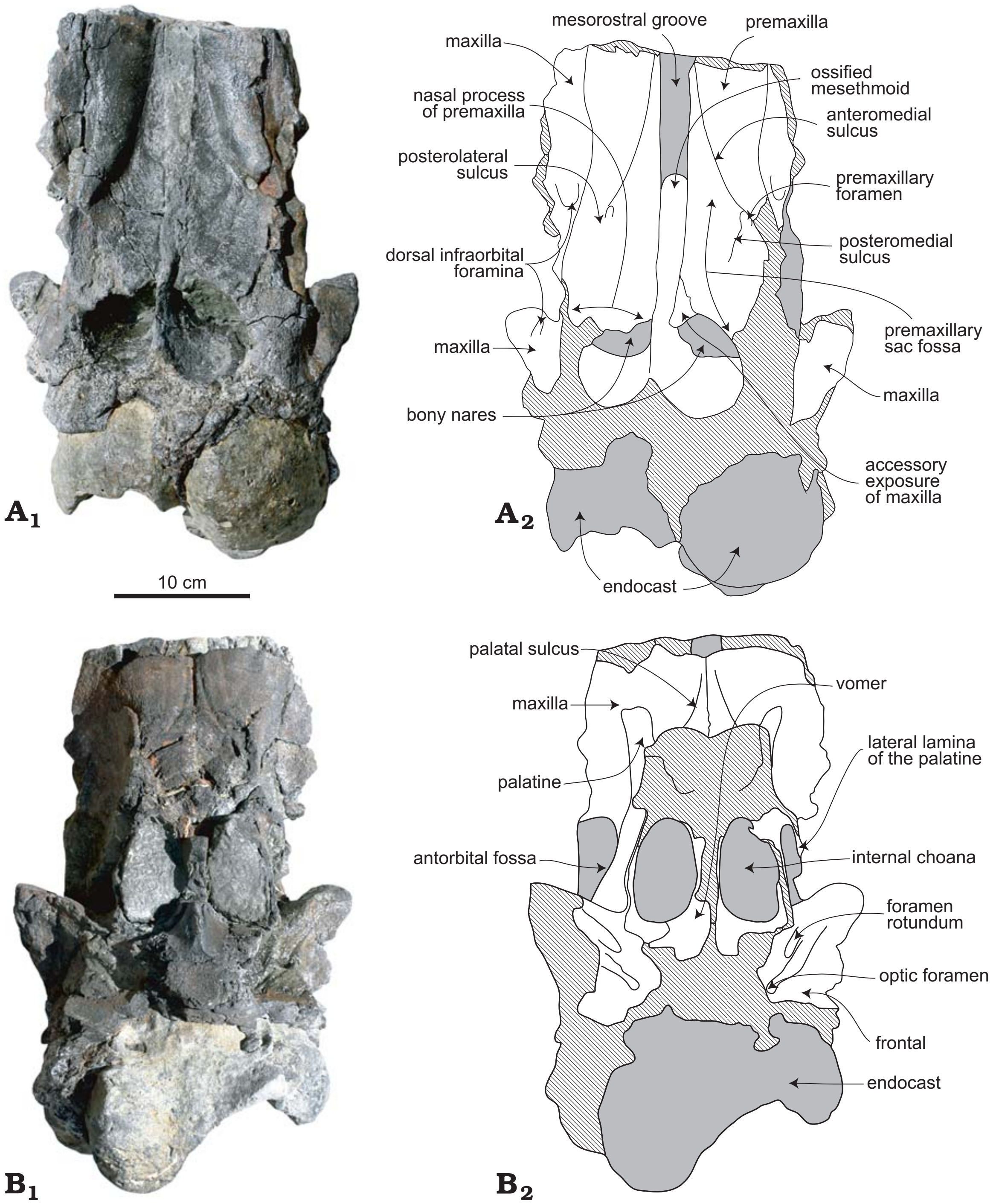

Fig. 2. Cranium of Globicephalinae gen. et sp. indet. 1 (UCMP 219223, Seacliff Beach skull), Pliocene, UCMP locality V99879, in dorsal (**A**) and ventral (**B**) views. Cross-hatching denotes damaged or missing bone, gray indicates matrix (including the endocast). Photographs (A_1, B_1), interpretative line drawings (A_2, B_2).

lary foramen occurs at the posterior end of the anteromedial sulcus and medial to the rostral surface of the premaxilla. The premaxillary sac fossae are wide, shallow, exhibit a cancellous bone texture, and form a transversely concave basin. Although both nasal processes of the premaxillae are damaged, the right appears to have been wider than the left at the midpoint of the external nares, judging from the raised platforms of the maxillae that the premaxillae would have sutured to. The posterior terminations of the nasal processes are not preserved.

Maxilla.—Much of the lateral part of the rostral portion of the maxilla is missing, and only a very small portion of the ascending process remains on either side of the skull. The rostral portion is preserved as a thin sliver lateral to the rostral portion of the premaxilla (Fig. 2A). An accessory exposure of the maxilla lies medial to the right premaxilla and forms the anteromedial margin of the right naris. In dorsal view, the maxilla-premaxilla suture anterior to the anteriormost dorsal infraorbital foramen is slightly concave laterally. The anteriormost dorsal infraorbital foramen is positioned slightly more anteriorly on the right side than on the left one. The maxillae form a dorsoventrally deep palate (Fig. 3A_1) with a trapezoidal cross section, and are posterolaterally underlapped by the palatine. Lateral to the palatine, the ventral surface of the maxilla is flat and wide. The ventral infraorbital foramen is positioned anteriorly within the antorbital fossa, which in turn is floored by the lacrimojugal crest of the maxilla.

Vomer and mesethmoid.—The vomer is not clearly visible on the anterior broken surface of the rostrum. Within the bony naris, the internasal septum is rotated clockwise about its vertical axis; in the absence of any diagenetic compaction, this feature is interpreted as natural.

Frontal.—The ventral orbital crest of the frontal is oriented anterolaterally, and forms a precipitous vertical crest that anteriorly demarcates the posterior boundary of the antorbital fossa (Fig. 2B). The optic foramen is laterally confluent with the frontal groove. Another groove is present in the frontal anteromedial to the frontal groove, forming an anterolateral continuation of the foramen rotundum; the anteromedial margin of this groove is adjacent to the ventral orbital crest.

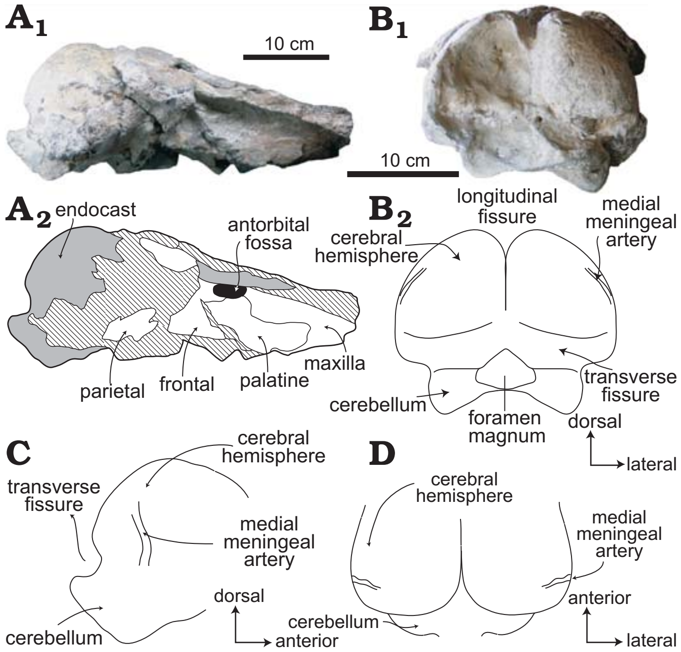

Fig. 3. Cranium of Globicephalinae gen. et sp. indet. 1 (UCMP 219223, Seacliff Beach skull), Pliocene, UCMP locality V99879, in lateral view, showing endocast (**A**). Endocast in posterior (**B**), lateral (**C**), and dorsal (**D**) views. Cross-hatching denotes damaged or missing bone, gray indicates matrix (including the endocast). Photographs (A_1, B_1), interpretative line drawings (A_2, B_2, C, D).

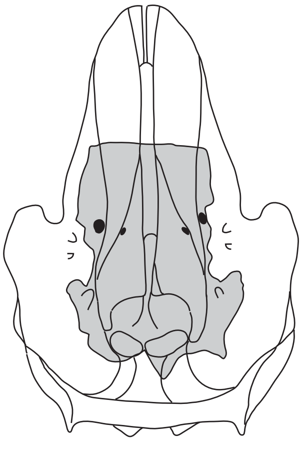

Fig. 4. Reconstruction of Globicephalinae gen. et sp. indet. 1, in dorsal view. Gray denotes the preserved portion of the cranium.

Palatine and pterygoid.— The ventral extremities of these elements are missing. The laterally compressed and dorsoventrally narrow maxillary process of the palatine extends anteromedial to the antorbital fossa. A transversely thin lateral lamina of the palatine projects posteriorly (Fig. 2B), parallel to the posterior medial lamina of the pterygoid, demarcating the pterygoid sinus fossa.

Posterior braincase and basicranium.—Residual fragments of the parietals and alisphenoids adhere to recesses of the braincase endocast. A remnant of a well-developed internal sagittal crest is preserved between the cerebral hemispheres of the endocast. In *Stenella attenuata*, the internal sagittal crest actually represents the ossified falx cerebri of the dura mater (Nojima 1988), and this appears to be the case in many other delphinids as well (Brian Beatty, personal communcation 2009), including the Seacliff Beach skull. Similarly, bony fragments preserved ventral to the region of the endocast corresponding to the right cerebral hemisphere are interpreted as ossified remnants of the tentorium cerebelli.

Endocast.—The right side of the brain endocast is nearly complete, with a slightly abraded and damaged surface (Fig. 3A, B). The cerebral hemispheres are large, subspherical, and separated medially by the internal sagittal crest/ossified falx cerebri (Fig. 3B–D). The cerebral hemisphere is separated from the cerebellum by a transverse fissure (sensu Colbert et al. 2005). On the lateral surface of the cerebral hemisphere, a faintly preserved ridge preserves the impression of the vertically oriented middle meningeal artery. The cerebellum appears to have been ventrally concave, and dorsoventrally thickened laterally near the cranial hiatus. The anteroventral apex of the cerebellar cast likely includes part of the cranial hiatus.

Gen. et sp. indet. 2

Fig. 2.

Material.—UCMP 219487 and 219488, two left petrosals collected from the pebble marker bed (UCMP locality V99869, northern shore of Monterey Bay, USA) by Stanley Jarocki (Watsonville, California, USA). Mio-Pliocene Purisima Formation, early to middle Pliocene (4.5–3.5 Ma).

Description.—The two isolated left petrosals resemble each other, and are inferred to represent the same taxon (Fig. 5). Petrosal measurements are presented in Table 2. In dorsal view, the outline of the petrosal is sigmoidal, with an anteromedially directed anterior process, a laterally thickened parabullary ridge, a medially convex pars cochlearis, and a posterolaterally projecting posterior process. In ventral view, the pars cochlearis is globular with a round medial margin. The ventral surface of the pars cochlearis is nearly flat. A sub-

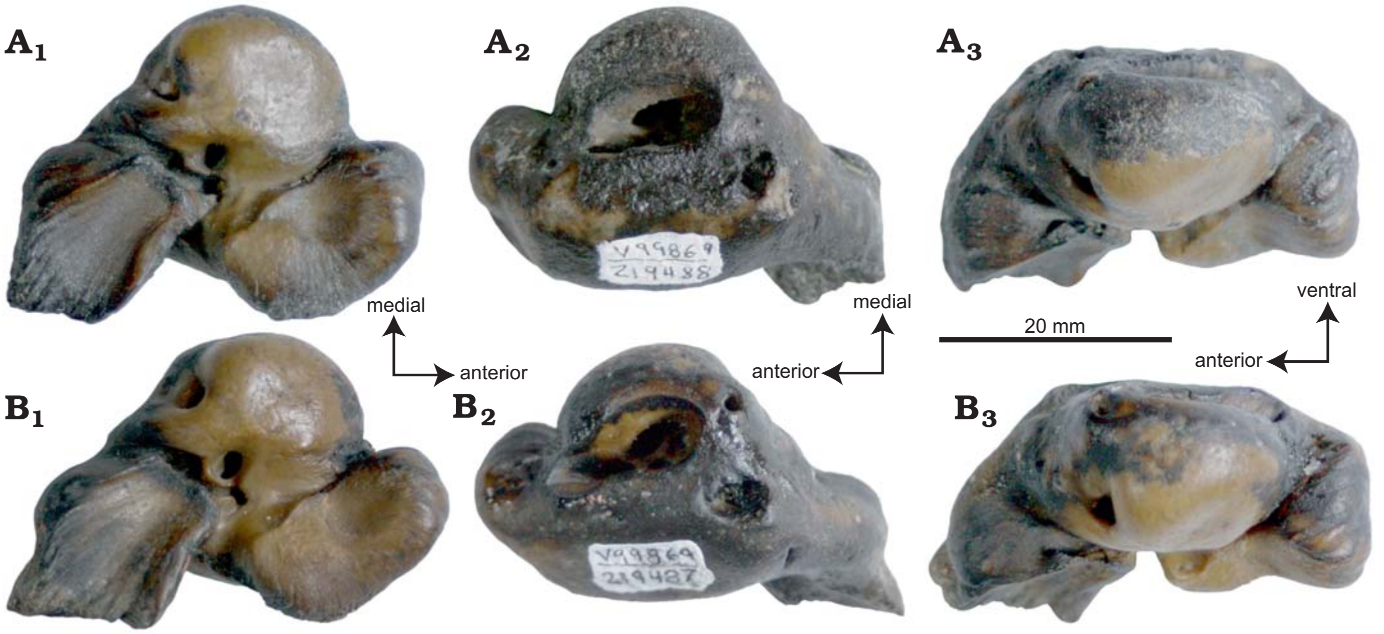

Fig. 5. Petrosals of Globicephalinae gen. et sp. indet. 2, early Pliocene, UCMP locality V99869. **A**. UCMP 219487, in ventral (A_1), dorsal (A_2), and medial (A_3) views. **B**. UCMP 219488, in ventral (B_1), dorsal (B_2), and medial (B_3) views.

tle, anteroposteriorly aligned ridge extends from the margin of the fenestra rotunda, medial to which the pars cochlearis is slightly concave. The aforementioned ridge is much more apparent in UCMP 219488. The fenestra rotunda is D-shaped, with its flat edge positioned dorsally. The fenestra rotunda is confluent with a dorsally directed, V-shaped furrow.

The long axis of the fenestra ovalis is oriented anteromedially-posterolaterally. Lateral to the fenestra ovalis is the distal opening of the facial nerve canal. The stapedial muscle fossa and the facial sulcus are separated by a minute ridge in UCMP 219487, but not in 219488. The stapedial muscle fossa is narrow and elongate in both specimens, and not excavated beyond the level of the dorsal margin of the fenestra rotunda. The internal acoustic meatus is anteroposteriorly elongate (Fig. 5A_2, B_2), owing to the inclusion of the facial nerve canal within the meatus. The meatus is teardrop-shaped, pointing anteriorly. The foramen singulare is medial to the spiral cribriform tract, with the partition separating the two being much lower than the transverse crest. The dorsal crest is not developed.

The anterior process is stocky and short, measuring approximately 81–90% of the length of the pars cochlearis (Fig. 5A_1, A_3, B_1, B_3; Table 2). The parabullary ridge is pronounced and overhangs more dorsal portions of the lateral side of the petrosal. In lateral view, the ventral margin of the anterior process is concave. The anterior margin of the anterior process is straight, giving the entire process a squared-off appearance. In anterior view, the anterior process appears triangular with ventral, dorsal, and medial apices.

The posterior process is relatively long (64 and 85% of the length of the promontorium in UCMP 219488 and 219487, respectively; Table 2) and projects posterolaterally (Fig. 5A_1, B_1). Its ventral side is dominated by a large, transversely concave, pentagonal posterior bullar facet with longitudinal grooves. The apex of the pentagon points posterolaterally, and its base parallels the trough that includes the facial nerve sulcus and stapedial muscle fossa. The angle formed between the anterolateral edge of the posterior bullar facet and the lateral edge of the body of the petrosal in ventrolateral view is ca. 90º and 100º in UCMP 219487 and 219488, respectively. Note, however, that measurement of angles is highly sensitive to slight differences in viewing perspective. Anteriorly, the posterior process is separated from the parabullary ridge by a deep hiatus epitympanicus.

Comparisons between specimens.—Despite the similarities between UCMP 219487 and 219488, some differences are evident dorsally. The edge of the internal acoustic meatus is more elevated in UCMP 219487 and the posterior margin is slightly pointed, whereas that edge is more rounded (but likely also abraded) in UCMP 219488. The aperture of the cochlear aqueduct in UCMP 219487 occurs on a low tuberosity (as in extant *Globicephala*); this structure is absent in UCMP 219488, and also appears to be abraded. The expanse of the pars cochlearis medial to the internal acoustic meatus is wider in UCMP 219488. In both specimens, the region lateral to the internal acoustic meatus is low and faces dorsally; how-

Table 2. Measurements of petrosals (in cm) of Globicephalinae gen. et. sp. indet. 2.

Measurement	UCMP 219487	UCMP 219488
Anteroposterior length	3.79	3.33
Length of pars cochlearis	1.49	1.52
Transverse width of internal acoustic meatus	0.54	0.63
Anteroposterior length of internal acoustic meatus	1.40	1.13
Length of anterior process	1.87	1.41

ever, in UCMP 219487 this region is flat, whereas in UCMP 219488 it is gently convex. As the dorsal face of the petrosal varies appreciably among extant delphinids (and cetaceans in general), these differences between UCMP 219487 and 219488 are attributed to intraspecific variation, as well as abrasion of the dorsal pars cochlearis in UCMP 219488.

Our regression analysis showed that the maximum width of the bony nares in delphinidans significantly increases with the length of the promontorium ($p < 0.001$), and resulted a line with a slope of 7.9852 and a y-intercept of -57.559 (Fig. 6). This equation slightly changes if it is based only on delphinids ($n = 33$, slope = 7.2787, y-intercept = -39.685) or globicephalines ($n = 12$, slope = 7.3159, y-intercept = -41.864). The Seacliff Beach skull has a maximum narial width of approximately 110.5 mm, which, based on the equation above, should be associated with a petrosal that has a promontorium 21 mm in length. By contrast, the promontoria in UCMP 219487 and UCMP 219488 are much smaller (14.95 and 15.24 mm, respectively; Fig. 6). This difference in size is not easily explained as the result of ontogeny, because in extant *Globicephala* the petrosal, and particularly the pars cochlearis, initially ossifies at near adult size, and the length of the petrosal shows no correlation with total body length (Kasuya 1973). Thus, our analysis indicates the presence of at least two globicephalines in the Purisima Formation.

The maximum nares width we measured is likely an overestimate, because the premaxillae are damaged. In most extant delphinids, a medial shelf of the ascending process of the premaxilla overhangs the lateral margin of the bony nares, somewhat narrowing their transverse width. It seems unlikely that, if preserved, the premaxillae would have reduced the width by 45 mm (i.e., 41%), which would be required to bring the petrosals and the Seacliff Beach skull in line with the proportions seen in other delphinidans. Nevertheless, given the appreciable scatter around the best fit line ($r^2 = 0.51954$), it is possible, although unlikely, that the fossils we describe represent a single taxon with a proportionally small petrosal and/or unusually large external bony nares. More complete specimens are needed to test our hypothesis that the skull and petrosals represent separate taxa.

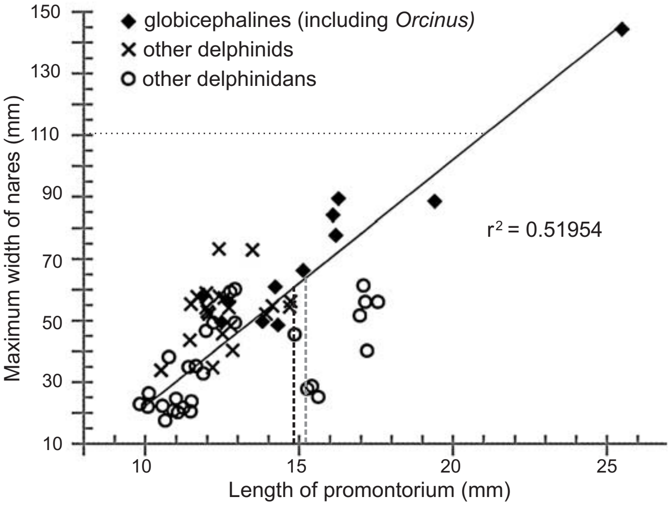

Fig. 6. Plot of maximum width of external bony nares versus length of promontorium for 62 delphinidan specimens, representing 34 species. Solid line is a reduced major axis regression (for all Delphinida). Horizontal dotted line is the nares width for the Seacliff Beach skull (UCMP 219223) and the vertical dashed lines are the lengths of the promontoria in UCMP 219488 (black) and 219487 (gray). In order to maximize the measurement area occupied by the specimens we sampled, the labeled y axis does not pass through the origin, but instead x = 8.

Discussion and conclusions

Comparisons and systematic placement of the Seacliff Beach skull.—This specimen exhibits at least one delphinid synapomorphy–asymmetrical ascending processes of the premaxillae, where the right ascending process is wider than the left, and the left premaxilla terminates further anteriorly and is not in contact with the left nasal (Barnes 1990). Although the ascending processes of the premaxillae are incomplete, the broken portion of the platform of the maxilla that supported the left ascending process appears to have been transversely constricted, suggesting the overlying premaxilla was also narrow (Fig. 2A). Referral of the Seacliff Beach skull to Globicephalinae is supported by its large size relative to non-globicephaline delphinids, and the presence of an anteriorly widening premaxilla on the rostrum, a globicephaline synapomorphy according to Muizon (1988), Bianucci (2005), and Aguirre Fernández et al. (2009). We compared the Seacliff Beach skull with modern and fossil delphinids, as well as modern and fossil monodontids owing to the presence of large, globicephaline-convergent monodontids in eastern North Pacific strata of upper Miocene and Pliocene age (Barnes 1977, 1984).

The Seacliff Beach skull differs from all monodontids by lacking deeply entrenched anteromedial and posterolateral sulci on the premaxilla, and by lacking a continuous exposure of the maxilla anterior to and along the lateral margin of the bony nares. The new specimen differs from *Denebola* and *Delphinapterus*, but resembles *Bohaskaia*, in having anteriorly diverging premaxillae. At the middle of the rostrum, the dorsal surface of the premaxilla faces dorsomedially (as in *Globicephala*), whereas in monodontids the premaxilla faces dorsolaterally.

The Seacliff Beach skull is substantially larger than most non-globicephaline delphinids. It is also larger than the globicephalines *Grampus*, *Feresa*, *Orcaella*, and *Peponocephala*, but similar in size to *Globicephala* and *Pseudorca*. The skull shares many morphological features with globicephalines, including a narrow median exposure of the maxillae between the premaxillae immediately anterior to the bony nares (smaller than in *Globicephala* and *Orcaella*, larger than in *Grampus*, *Orcinus*, but resembling *Peponocephala* and *Pseudorca*; also present in some *Tursiops*), a medially sloping dorsal surface of the premaxilla in the middle of the rostrum (present in *Globicephala*, *Orcinus*, *Platalearostrum*, *Protoglobicephala*, and

Pseudorca), and a relatively wide premaxilla. An additional feature that allies this specimen with globicephalines is the convex lateral margin of the ascending process of the premaxilla: in most non-globicephaline delphinids and monodontids, but also *Grampus* and *Globicephala*, this margin is straight.

Similar to *Globicephala*, *Platalearostrum*, and *Protoglobicephala*, but unlike all other globicephalines, the Seacliff Beach skull exhibits an anteriorly widening premaxilla. However, the Seacliff Beach skull differs from *Protoglobicephala* in possessing a relatively wider exposure of the maxilla on the rostrum, and from all globicephalines and other delphinids in having well-developed ridges on the rostral surface of the premaxilla. The Seacliff Beach skull differs from *Grampus* in the absence of premaxillary eminences, and from *Peponocephala* in having strap-like anterior palatine crests. In most globicephalines (including the Seacliff Beach skull), the anteriormost dorsal infraorbital foramen is located anterior to the premaxillary foramen. By contrast, the opposite is true for *Arimidelphis*, *Feresa*, *Orcaella*, and *Protoglobicephala*, while *Orcinus* further differs in exhibiting two premaxillary foramina. In conjunction with other aspects of cranial asymmetry, the mesethmoid septum is twisted clockwise about its vertical axis in the Seacliff Beach skull (in dorsal view). This also the case in *Globicephala*, *Peponocephala*, *Protoglobicephala*, and *Pseudorca*, whereas the septum is straight and anteroposteriorly aligned in *Arimidelphis*, *Orcinus*, and all other globicephalines.

The Seacliff Beach skull shares many similarities with *Pseudorca*, including a weakly developed fossa for the postorbital lobe of the pterygoid sinus (in other globicephalines, this fossa is larger in concert with more widely flaring lateral laminae of the palatines), an anteroposteriorly elongate antorbital fossa, and a deep posterior portion of the palate with a trapezoidal cross section. Unlike *Pseudorca*, however, the Seacliff Beach skull seems to preserve no alveoli in the posterior portion of the maxilla. It remains unclear whether teeth, if present, were only present further anteriorly (as in *Protoglobicephala*), or whether the maxilla was relatively wider than in *Pseudorca* and the tooth-bearing parts have merely been eroded away.

In summary, the Seacliff Beach skull has numerous features in common with *Globicephala*, *Feresa*, and *Pseudorca* to the exclusion of all other odontocetes, and is thus here referred to the Globicephalinae. The particular combination of characters displayed in this fossil precludes its assignment to any extant delphinid genus, and clearly indicates that it is a new species. Among known taxa, the dorsal side of the skull is most similar to *Globicephala*, whereas the ventral side resembles *Pseudorca*, suggesting it may be assignable to the *Globicephala* + *Pseudorca* + *Feresa* clade (sensu Aguirre Fernandez et al. 2009). Although the Seacliff Beach skull adds to our knowledge of Pliocene odontocete assemblages, it is too incomplete to designate a new taxon at this time.

Comparisons and systematic placement of the referred petrosals.—The two isolated petrosals (UCMP 219487 and 219488) were compared to the petrosals of delphinids and monodontids. Features of the Purisima petrosals are similar to those of some monodontids and the delphinid *Globicephala*. First, the well-developed parabullary ridge and elongate posterior process of the Purisima petrosals also characterize *Monodon* (AMNH 73315, 19318, 16733) and *Globicephala melas* (AMNH 34934, 185106). Second, as in the Purisima petrosals, *Monodon* and *Globicephala* have an extension of the hiatus epitympanicus that excavates the anterolateral side of the posterior process. By contrast, the parabullary ridge is not as well developed, the posterior process is much shorter, and the tegmen tympani is not excavated on its lateral side in other globicephalines (e.g., *Feresa*, USNM 504916, 571268; *Peponocephala*, USNM 504505, 550399).

The anterodorsal angle of the anterior process in both *Monodon* and *Globicephala* is elongate and forms a distinct spine. By contrast, the anterior process in the Purisima petrosals is very short and stout with a blunt dorsolateral apex, thus resembling the morphology of some delphinines (e.g., *Delphinus delphis*, AMNH 100127; *Tursiops truncatus*, AMNH 180808, 212554). Furthermore, although certain aspects of the Purisima petrosals are superficially similar to those of *Monodon*, several differences in the endocranial foramina are apparent. In *Monodon*, the facial nerve canal is positioned lateral to the internal acoustic meatus, whereas it is well anterior to the meatus in UCMP 219487 and 219488. The internal acoustic meatus is circular and surrounded by an elevated rim with minute projections in *Monodon*, *Delphinapterus*, and *Denebola*. By contrast, the Purisima petrosals, like those of other delphinids, have an elongate internal acoustic meatus with a low rim. Based on the above comparisons, the Purisima petrosals are most similar to those of delphinids, particularly those of *Globicephala*.

Globicephaline diversification and dispersal.—Recent molecular studies suggest a late Miocene (ca. 9–10 Ma) divergence time for Delphinidae (McGowen et al. 2009; Cunha et al. 2011; Vilstrup et al. 2011). Although the deepest divergences in the delphinid clade date to the late Miocene, Bianucci (2013) noted that the number of cladogenetic events increases through time, and that the majority of nodes seem to arise during the late Pliocene and Pleistocene. Although the Purisima globicephalines are too young to weigh in on the age of the delphinid divergence, they have implications for molecular-based divergence dating of the Globicephalinae, variously estimated at 8 Ma (late Miocene; Vilstrup et al. 2011), 5.5 Ma (latest Miocene; Cunha et al. 2011), or 4 Ma (early Pliocene; McGowen et al. 2009).

Globicephalines were already widespread and diversified during the early Pliocene (Fig. 7), suggesting that the estimate of 4 Ma (McGowen et al. 2009) is too young. In fact, it is possible that the material described here may be even older (i.e., 3.5–5.6 Ma), although this discrepancy could be resolved if the Purisima fossils were excluded from the globicephaline crown group. A similar explanation has recently been suggested for the age of some fossil delphinines (Bianucci 2013). We suspect that the divergence date of 8 Ma

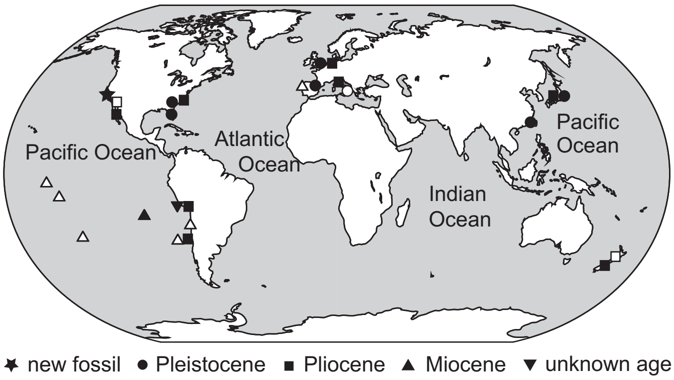

Fig. 7. Global map of globicephaline fossil occurrences. Closed symbols denote figured or described fossils; open symbols denote records not described or figured. Records compiled from sources listed in the SOM available at http://app.pan.pl/SOM/app60-Boessenecker_etal_SOM.pdf

reported by Vilstrup et al. (2011) is too old, considering that most globicephalines are at least 2 Ma younger, and that the 8 Ma estimate falls inside one of the most intensively sampled geologic stages for fossil cetaceans (Uhen and Pyenson 2007). A possible exception might be *Hemisyntrachelus oligodon*, which was recently transferred from *Tursiops* to *Hemisyntrachelus* by Post and Bosselaers (2005) and as such may have globicephaline affinities (Bianucci 2005; Aguirre Fernandez et al. 2009; Murakami et al. 2012a).

Hemisyntrachelus oligodon was described from the Sud-Sacaco locality of the Pisco Formation (Pilleri and Siber 1989), originally considered to be early Pliocene in age (Muizon and de Vries 1985), but now thought to be late Miocene (7.1–5.93 Ma) based on strontium isotope and paleomagnetic dating (Ehret et al. 2012). However, *Hemisyntrachelus* may be a junior synonym of the delphinine *Tursiops* (Barnes 1990). If *Hemisyntrachelus oligodon* is considered to be a globicephaline, the late Miocene (8 Ma) divergence date of Vilstrup et al. (2011) is probably appropriate; however, if future studies demonstrated that *Hemisyntrachelus oligodon* is a species of *Tursiops,* as originally published by Pilleri and Siber (1989), or if *Hemisyntrachelus* were found to be a junior synonym of *Tursiops* (Barnes 1990), then the globicephaline fossil record would be most consistent with the 5.5 Ma divergence date estimate of Cunha et al. (2011).

The distribution and age of globicephaline fossils indicates that the clade had not only fully diversified by the early Pliocene, but that by this time it was already globally widespread. Fossil globicephalines of Pliocene age are present in the USA (California, South Carolina, North Carolina), Chile, England, Italy, Japan, Mexico, the Netherlands, and Spain (Fig. 7; SOM), indicating widespread presence in the North and South Pacific, North Atlantic, and Mediterranean. Fossils assignable to extant globicephaline genera (e.g., *Pseudorca* sp., *Globicephala* sp.), in concert with the phylogenetic placement of extant pilot whales and false killer whales as the most derived globicephalines (McGowen et al. 2009; McGowen 2011; Vilstrup et al. 2011), suggest diversification of the whole subfamily by the early Pliocene. Unfortunately, geographically widespread Pliocene globicephaline fossils also make it impossible at present to identify a center of origin for the clade. Future discoveries of unequivocal, late Miocene globicephalines would help clarify when and where this group of large-bodied delphinids originated.

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